Palaeogeography, Palaeoclimatology, Palaeoecology 512 (2018) 95–105

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

The occurrence of *Burretiodendron* from the Oligocene of South China and its geographic analysis

Jun-Ling Dong [a], Bai-Nian Sun [a,*], Teng Mao [a], Chun-Hui Liu [a], Xue-Lian Wang [a], Ming-Xuan Sun [b], Fu-Jun Ma [c], Qiu-Jun Wang [d]

[a] School of Earth Sciences & Key Laboratory of Mineral Resources in Western China (Gansu Province), Lanzhou University, Lanzhou 730000, China
[b] School of Electrical Engineering and Computer Science, Louisiana State University, Baton Rouge, LA 70803, USA
[c] School of Geography and Tourism, Guizhou Education University, Guiyang 550018, China
[d] Guizhou Research Centre for Paleontology, College of Resource and Environmental Engineering, Guizhou University, Guiyang 550003, China

ARTICLE INFO

Article history:
Received 3 March 2017
Received in revised form 27 June 2017
Accepted 6 July 2017
Available online 12 July 2017

Keywords:
Karstification
Ecology
Paleoclimate
Fruits

ABSTRACT

The fossil records of *Burretiodendron* Rehder are reviewed based on diagnostic winged fruits from the Oligocene Ningming Formation, Guangxi, South China. Today, this genus is endemic to Southeast Asia with six extant species that are well distributed in limestone mountain forests under a monsoonal climate. The fossil records of this genus were represented only in Yunnan of southwestern China. The fossil fruits are assigned to a new species, *Burretiodendron guangxiensis* J.L. Dong et B.N. Sun sp. nov., are smaller than those of living species. *Burretiodendron* is a good indicator of paleoclimate and karstification due to its restricted distribution which is determined by specific temperature, precipitation and the topographic condition. We investigated the climate requirements of *Burretiodendron*. It is possible to accurately infer that the Ningming paleoflora represented a warm and humid climate with seasonal precipitation during the Oligocene. Edaphic preferences of the nearest living relative identified for the fossil species may point to the existence of a karstic system in the Ningming Region during the Oligocene.

© 2017 Elsevier B.V. All rights reserved.

1. Introduction

Burretiodendron Rehder (Malvaceae s.l.) is a rare tree genus that is endemic to tropical Southeast Asia (Fig. 1) with six living species. They are primarily distributed in limestone mountain forests with a monsoonal climate on the Sino-Vietnamese border (including Guangxi, Yunnan, Guizhou of southwestern China, and Tonkin of northern Vietnam), and in the northern Malay Peninsular in Thailand and Myanmar (Zhuge, 1990; Li et al., 2004; Anberrée et al., 2015). This region is the biodiversity centre of extant species on the Sino-Vietnamese border, and there are five species living here in total: *Burretiodendron hsienmu* Chun & K.C. How, *B. obconicum* Chun & K.C. How, *B. esquirolii* (H. Lév.) Rehder, *B. kydiifolium* Y.C. Hsu & R. Zhuge and *B. brilletii* Kosterm. Only one species, *B. siamense* Kosterm, is distributed in the North Malay Peninsula in Thailand and Myanmar. *Burretiodendron* was originally established by Alfred Rehder (1936) and treated within the Tiliaceae. Due to limited materials and a lack of further clarification, in-depth studies for this genus have not been conducted except for their gross morphology (Chang and Miau, 1978; Zhuge, 1990; Tang et al., 2005a) and a palynological investigation (Tang and Gao, 1993). Currently, *Burretiodendron* is placed in the subfamily Dombeyoideae of the Malvaceae s.l. Jussieu based on detailed morphological characteristics, molecular studies and plastid DNA analyses (Judd and Manchester, 1997; Alverson et al., 1999; Bayer et al., 1999; Won, 2009; Bell et al., 2010). Although *Burretiodendron* is diverse and widely distributed in tropical Southeast Asia, its fossil record is limited. There is no known pollen or wood of Cenozoic age attributable to this family. The only reliable record is known as the leaves and fruits from the upper Miocene Xiaolongtan Formation (Wenshan and Maguan) of southeastern Yunnan, China (Anberrée et al., 2015).

Burretiodendron is an extraordinary precious commercial tree species and a medicinal plant with rich nutrient elements. The wood of *Burretiodendron* can be made into chopping blocks, advanced furniture, and shipping products. Some elements, contained in the seed, can effectively improve the human immune system and enhance life vitality. *Burretiodendron hsienmu* and *B. esquirolii* are excellent afforestation species for limestone mountains. They can improve soil fertility quality and have important scientific research values (Li et al., 2008). *Burretiodendron* exhibits highly diversity in Southeast Asia (between 30°N and 10°N) and embraces a confined distribution range of physiological tolerance in tropical mountain rainforests. It prefers thermophilic and alkaline soil environments. Moreover, *Burretiodendron* is also one of the most representative vegetation elements in tropical seasonal

* Corresponding author.
E-mail address: bnsun@lzu.edu.cn (B.-N. Sun).

http://dx.doi.org/10.1016/j.palaeo.2017.07.004
0031-0182/© 2017 Elsevier B.V. All rights reserved.

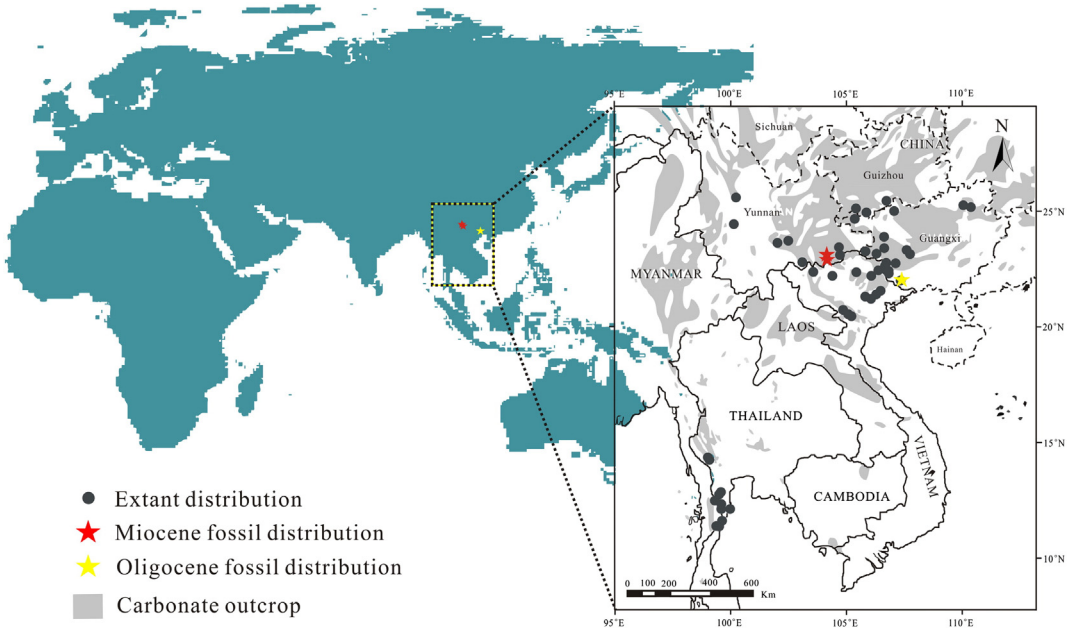

Fig. 1. Distribution map of extant and fossil *Burretiodendron* (following Anberrée et al., 2015). Red stars represent the Miocene fossil sites; yellow star represents the Oligocene fossil site.

rainforests (Li et al., 2008), and its distribution is dominated by climate, moisture and the topographic condition (Wang, 2012). The very restricted distribution and ecological habit of *Burretiodendron* make it particularly suitable to assess the paleoclimate of the Ningming Region in the Oligocene.

The karstic dynamic system represents an important part of the earth surface system (Yuan, 1997), and biological action is one of the most active geological agents in the earth surface system (Yin et al., 1994). Biogenetic karstification, particularly vegetation, is the most active factor affecting the rate of dissolution (Deng, 1982; Cao et al., 2001; Yuan, 2001). Plants can regulate the CO_2 concentration through photosynthesis and respiration (Hamilton and Frank, 2001; Li et al., 2008), and the secretions of roots and the decomposition of organic matters can produce a mass of organic acids, especially carbonic anhydrase, which can promote the dissolution of carbonate formation (Eisenhauer et al., 2012). Furthermore, plant is also one of the major factors of rock weathering and soil formation (Zhang, 1992). Karst vegetation emerges under conditions of the karstic geological environment (Li et al., 2003). In other words, as long as there is a karstic environment, a type of karst vegetation will emerge that is adapted to the local climate. *Burretiodendron hsienmu* is a relatively strong regional plant growing only in limestone mountain rainforests. Therefore, the study of *Burretiodendron* is of great significance to study the occurrence of the karstic system.

Here, we depict a new *Burretiodendron* fruit species from the Oligocene Ningming Formation of Ningming Basin, Guangxi Province, Southwest China. This is the oldest occurrence of fossil *Burretiodendron* from the Cenozoic of South China. This discovery indicates that *Burretiodendron* already existed in south China during the Oligocene. More comprehensive characteristics of the fruit morphology and the cuticles of the wing and endocarp are provided and the fossil records of *Burretiodendron* are reviewed. The paleoclimate, paleoecology and karstification implications of the Ningming Region during the Oligocene are also discussed.

2. Materials and methods

2.1. Geologic settings

Fossil fruits were collected from the Ningming County, Southwestern Guangxi, China. The strata belong to the Ningming Formation, which are dominated by grey-dark grey mudstones with light yellow shaly siltstones and fine-grained sandstones (Fig. 2B; Ning et al., 1994). The stratum strikes are in the northwest-southeast direction and the layers are gently inclined. There is no isotopic dating available and mammals are not hitherto found in the Ningming Formation. Ning et al. (1994) inferred a late Eocene–Oligocene age for the Ningming Formation based on lithostratigraphy. A palynostratigraphic study of the samples from the Ningming Formation indicates an Oligocene age, and the age of the Cenozoic deposits of the Ningming Basin may range from the late Eocene to the Oligocene (Wang et al., 2003). Well preserved fish (Chen et al., 2005; Chen and Chang, 2011) and plant macrofossils from the same locality reported in previous studies (Shi et al., 2010, 2014; Wang et al., 2014; Ma et al., 2015, 2016) also supported an Oligocene age, which is adopted in this paper.

2.2. Morphological study

A total of 18 fossil fruits of *Burretiodendron* were preserved as compression fossils and were collected from the Ningming Formation. The gross features were obtained using a Sony DSC-T70 digital camera and a Leica MZ 12.5 stereomicroscope. The extant comparative materials originated from the South China Botanical Garden Herbarium, Guangzhou, Chinese Academy of Sciences. The fruit length is the longest line parallel to the primary vein leading to the endocarp. The fruit width is the widest line perpendicular to the primary vein. The cuticles of the fossil and extant specimens were prepared according to the conventional methods described by Dong et al. (2015). The terms for the specimen description of the fruits follow Harris and Harris (2001) and are based on Conover (1991) for fruit cuticles. All of the specimens and LM slides are deposited in the Institute of Palaeontology and Stratigraphy, Lanzhou University, Gansu, China.

The cluster analysis was conducted using SPSS to determine the similarity of the fruit morphology between the present fossils and the modern species with the aim of identifying the nearest living relative (NLR) of the present fossils. *B. brilletii* is excluded in the morphological comparison because its morphological data are still unknown. We selected 5 living species for further comparison based on the gross morphology. The cluster analysis is built based on 7 fruit characteristics for each species including: 1) Fruit outline shape; 2) Fruit outline base; 3) Endocarp

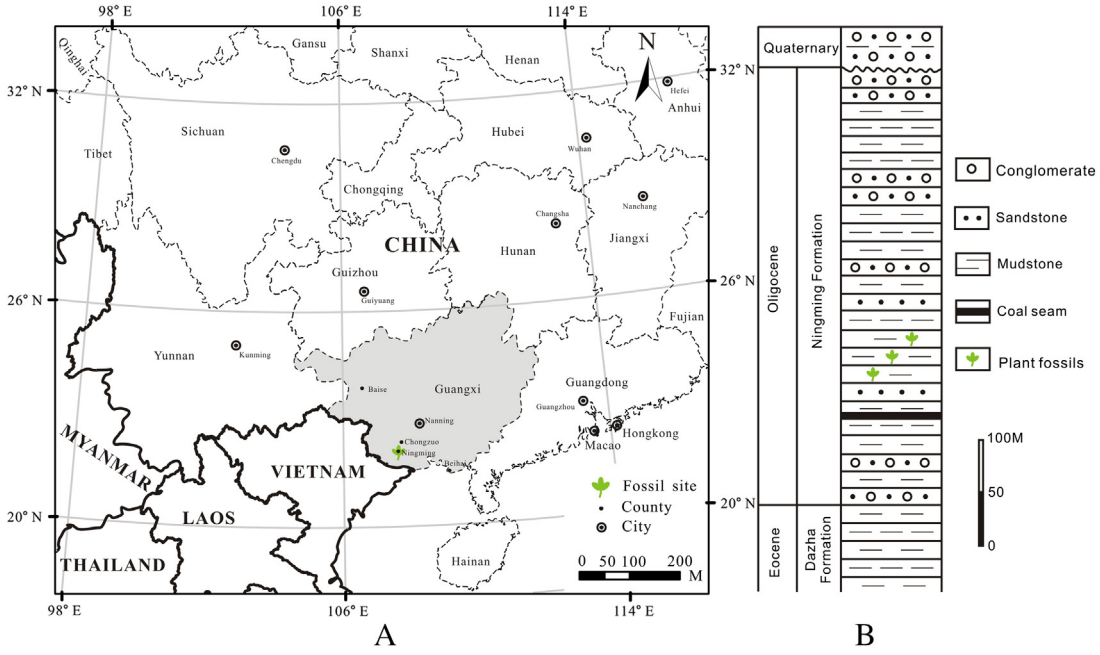

Fig. 2. Map showing the fossil site (A) and the generalized stratigraphic section of the Ningming Formation (B; redrawn after Ning et al., 1994).

shape; 4) Fruit outline: L/W; 5) Endocarp: L/W; 6) Fruit length/Endocarp length: FL/EL; and 7) Fruit width/Endocarp width: FW/EW.

3. Results

3.1. Systematics

Family: Malvaceae Jussieu s.l.
Subfamily: Dombeyoideae Beilschmied.
Genus: *Burretiodendron* Rehder, 1936
Species: *Burretiodendron guangxiensis* J.L. Dong et B.N. Sun sp. nov.
Holotype: LDGSW–2014–300 (Fig. 3A–B).
Paratypes: LDGSW–2014–301 (Fig. 3C), LDGSW–2014–302 (Fig. 3D), designated here.
Repository: Institute of Palaeontology and Stratigraphy, Lanzhou University, Gansu, China.
Type locality: Ningming County, Guangxi, southwest China.
Etymology: The specific epithet *guangxiensis* is chosen in reference to the Guangxi Province where the fossil site is located.
Diagnosis: Fruits capsule, two-winged mericarp, obovate, base acuminate, apex rounded to retuse. A longitudinal, median carpellary suture line is prominent and strong. Wing veins fan outward into the wings from the obovate endocarp, straight, sinuous anastomosing and dichotomising in course but not forming elongated areoles. The endocarp is situated in the middle of mericarp, base cuneate, apex rounded on the abaxial view but retuse on the adaxial view. The distance between the base of the mericarp and the base of the endocarp is 4.0–6.5 mm. It is single-seeded and the traces borne by seed are visible.
Description: Fossils are preserved as two-winged mericarp compressions. The capsular valves are entire-margined and chartaceous. The fruits are obovate with a rounded to retuse apex and cuneate base (Figs. 3, 4), measure 11.8–18.2 mm long by 6.6–10.7 mm wide and have a length:width (L:W) ratio of 1.5–2.0. The endocarp is obovate with an acute base and rounded apex on the abaxial view but retuse on the adaxial view. The endocarp is situated in the centre of the mericarp, 4.4–6.5 mm long and 3.0–4.6 mm wide, and has a L:W ratio of 1.2–1.7. The distance between the base of the mericarp and the base of the endocarp is 4.0–6.5 mm. The main veins fan outward into the wings from the endocarp area, craspedodromous, anastomosing and dichotomising but not forming elongated areoles, and terminating directly at the distal margin of the wing. Furthermore, it is single-seeded (Fig. 4F) and the traces borne by seed (Fig. 3I) are visible.
The cuticles of the wing show dense trichome bases and sparse stomata, and the epidermal vein cells are isodiametric and elongated, often quadrangular to sometimes pentagonal and irregularly arranged (Fig. 5A–C, G–I), 10.0–26.2 μm long and 7.0–13.6 μm wide, L:W ratio of 0.9–3.1. The anticlinal walls are straight to slightly curved and the periclinal walls are smooth. The solitary celled trichome bases are evenly distributed, rounded, 8.9–15.1 μm in diameter, and are surrounded by six to nine radial and wedge-shaped epidermal cells. The stomatal complexes are irregularly distributed, randomly oriented, and anomocytic. The outer stomatal ledges are fusiform to elliptic in outline, 8.0 μm × 3.9 μm, and show a length to width ratio of 2.1 (Fig. 5C, I). The cuticles of the endocarp show fenstral fabric, quadrangle to pentagon (Fig. 5D–F). The anticlinal cell walls, oblique and straight, have two-layer structure and are sunken in the middle part (Fig. 5K–L).

3.2. Cluster analysis of *Burretiodendron guangxiensis* sp. nov.

The result of the cluster analysis dendrogram performed by SPSS indicates that *Burretiodendron hsienmu* is most similar to our fruit fossils in terms of their morphological characteristics (Fig. 6). In addition, the epidermal cells of the wing of *B. hsienmu* also show a random arrangement, isodiametric or elongated, often quadrangular to sometimes pentagonal. The anticlinal walls are straight or slightly curved and the periclinal walls are smooth (Fig. 7G–J). The solitary celled trichome bases are rounded, and are surrounded by five to eight radial and wedge-shaped epidermal cells. The stoma is randomly oriented and anomocytic (Fig. 7M–O). The cuticles of the endocarp show fenstral fabric that is quadrangle to pentagon with oblique and straight anticlinal cell walls. Similarities in both morphological characteristics and anatomical features indicate *B. hsienmu* is the nearest living relative of *B. guangxiensis* sp. nov.

3.3. The ecological requirements of *Burretiodendron hsienmu*

Burretiodendron hsienmu is an evergreen megaphanerophyte tree and a protected species in China. It is extensively distributed in Guangxi, Yunnan of south China and North Vietnam (Tang et al., 2005b). *B. hsienmu* is entirely restricted to the limestone mountain rainforests and is a characteristic species of limestone floras (Gao, 2006). It mainly

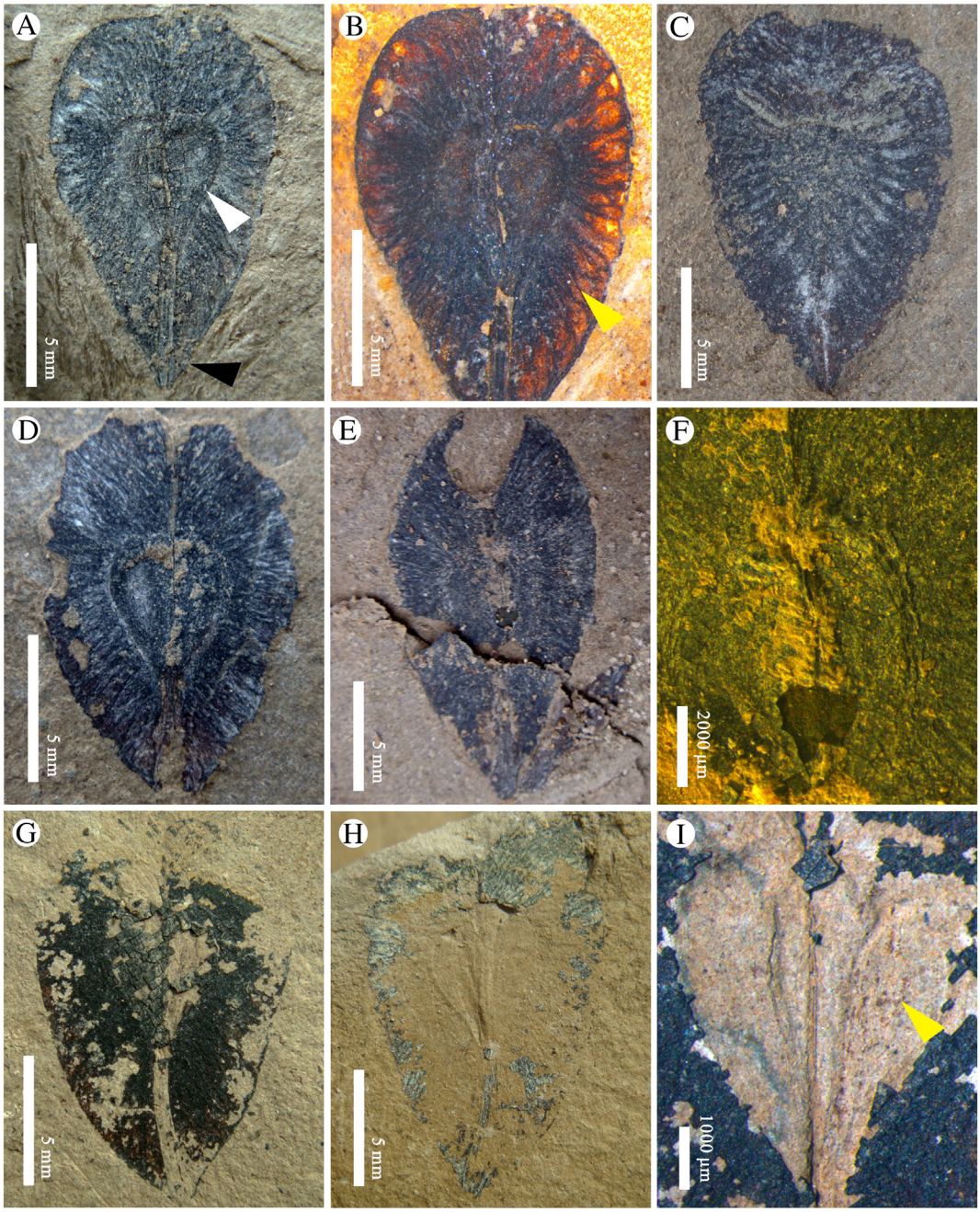

Fig. 3. *Burretiodendron guangxiensis* J.L. Dong et B.N. Sun sp. nov. (A–B) Adaxial view. Holotype. LDGSW–2014–300. (A) Obovate endocarp (white arrowhead) and cuneate base (black arrowhead). (B) The processing surface features showing straight, sinuous anastomosing and dichotomising wing venation (yellow arrowhead). (C) Abaxial view. Paratype. LDGSW–2014–301. (D) Adaxial view. Paratype. LDGSW–2014–302. (E–F) Abaxial view. (F) Enlargement of (E), showing an obovate endocarp. (G–H) Adaxial view. (I) Enlargement of (G), showing the traces borne by the seed (yellow arrowhead).

vegetates on steep slopes at altitudes from 150 to 900 m a.s.l., most commonly between 300 and 550 m (Wang et al., 1986; Zhuge, 1990; Tang et al., 2005b; Anberrée et al., 2015). *B. hsienmu* is found only in warm climate with the temperature of the coldest month between 10.9 °C and 13.9 °C and the warmest month ranging from 25.1 °C to 28.4 °C. The annual precipitation is as high as 1100 mm to 1500 mm, whereas the cold quarter fall is <50 mm (Wang et al., 1986). The roots of *B. hsienmu* are extremely developed and have a strong enough penetrating power to crack rocks. The distribution of *Burretiodendron* is directly affected by the karst dynamic system (Wang, 2012). Furthermore, the growth of *B. hsienmu* can aggravate the occurrence of karstification and enhance the speed of rock weathering and soil formation (Li, 2002).

4. Discussion

4.1. Systematic assignment of the fruit fossils

The studied fruits are characterized by the presence of capsules with two-winged valves, an obovate outline with rounded to retuse apex and cuneate base. These characteristics are extremely similar to *Craigia* W.W. Sm. & W.E. Evans, so that they are sometimes confounded (Chun and How, 1956; Kostermans, 1961). However, *Burretiodendron* is readily distinguished from *Craigia* by distinctive fruits. *Craigia* fruits are mainly elliptic outline with a rounded base and inwardly concave into the central axis of fruit body (Long et al., 1985; Tang et al., 2005a). The main veins radiate from the midline of each valve. In

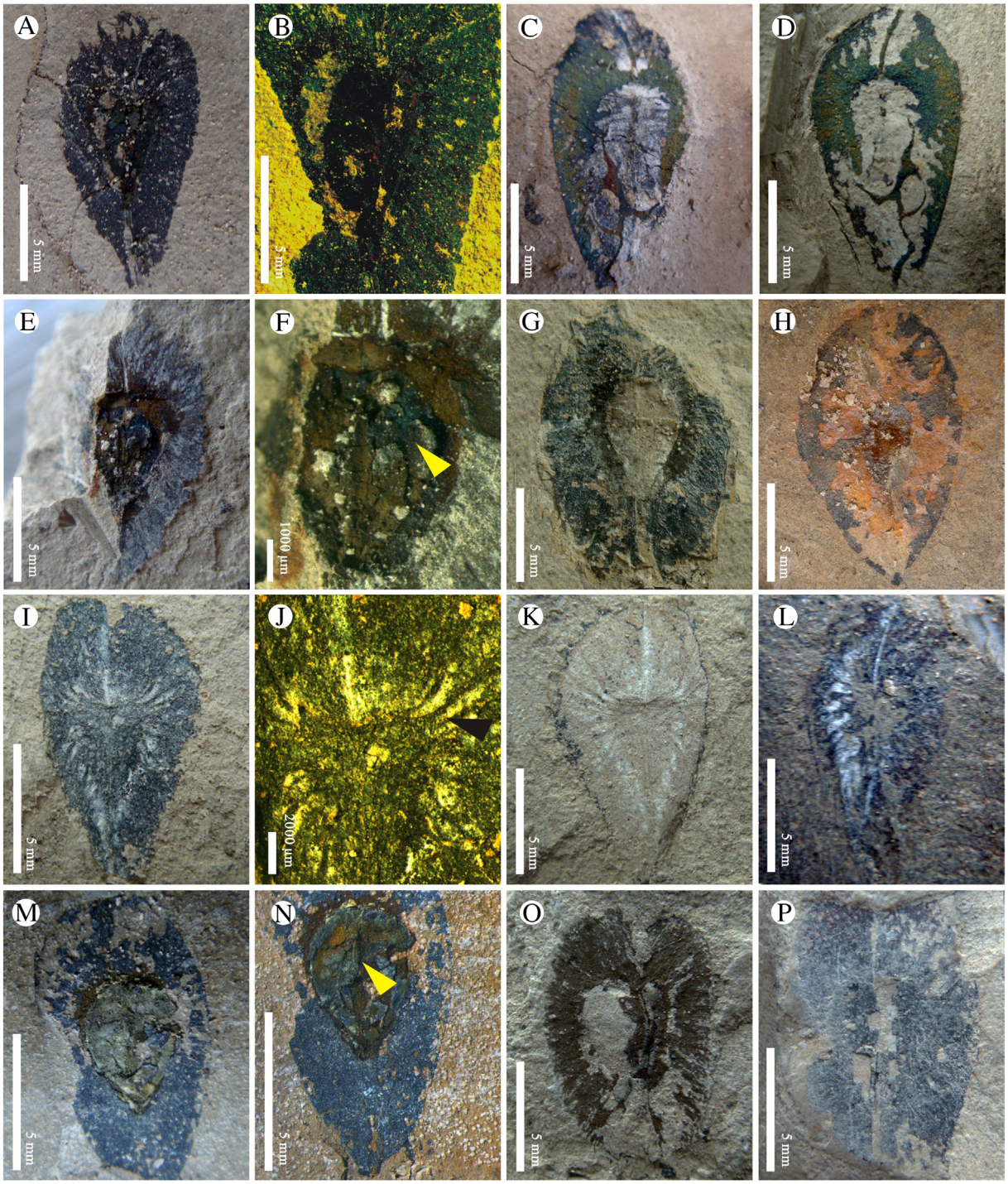

Fig. 4. *Burretiodendron guangxiensis* J.L. Dong et B.N. Sun sp. nov. (A–B, E–G, M–P) Adaxial view. (C–D, H, I–L) Abaxial view. (B) Enlargement of (A), showing obovate endocarp on the adaxial view. (F) Enlargement of (E), showing the obovate seed (yellow arrowhead). (J) Enlargement of (I), showing the obovate endocarp and craspedodromous, anastomosing and dichotomising wing venation. (N) Enlargement of (M), showing the septum in the locule area (yellow arrowhead).

addition, the wing venation is sparse, craspedodromous to fimbrial vein, dichotomizing and anastomosing to form elongated areoles with occasionally branched freely ending veinlets (Manchester and O'Leary, 2010). The crucial distinction is the locular shape that is oblong fusiform to elliptical in *Craigia* and obovate in *Burretiodendron* (Bůžek et al., 1989; Kvaček et al., 1991).

These characteristics, namely, that veins fan outward into the wings from the fruit body and wing venation is dichotomizing and anastomosing, are presented in most families (O'Leary, 2007; Manchester and O'Leary, 2010; Herrera et al., 2014), such as *Fortuynia* Schuttlew. ex Boiss. (Brassicaceae), *Lophopyxis* Hook (Lophopixidaceae), the genera *Combretum* Loefl., *Terminalia* L., and *Pteleopsis* Engl. (Combretaceae), *Podopterus* Bonpl. (Polygonaceae), the genera *Pentace* Hassk., *Maxwellia* Baill. (Malvaceae) and *Tetrapterocarpon* Humbert (Fabaceae). Nevertheless, it is noteworthy that these genera differ from *Burretiodendron* based on their subparallel and much denser wing venation. The locular shape is fusiform in *Combretum*, *Terminalia*, *Pteleopsis*, *Maxwellia* and *Tetrapterocarpon*. Beyond that, the wing of *Maxwellia* is thick,

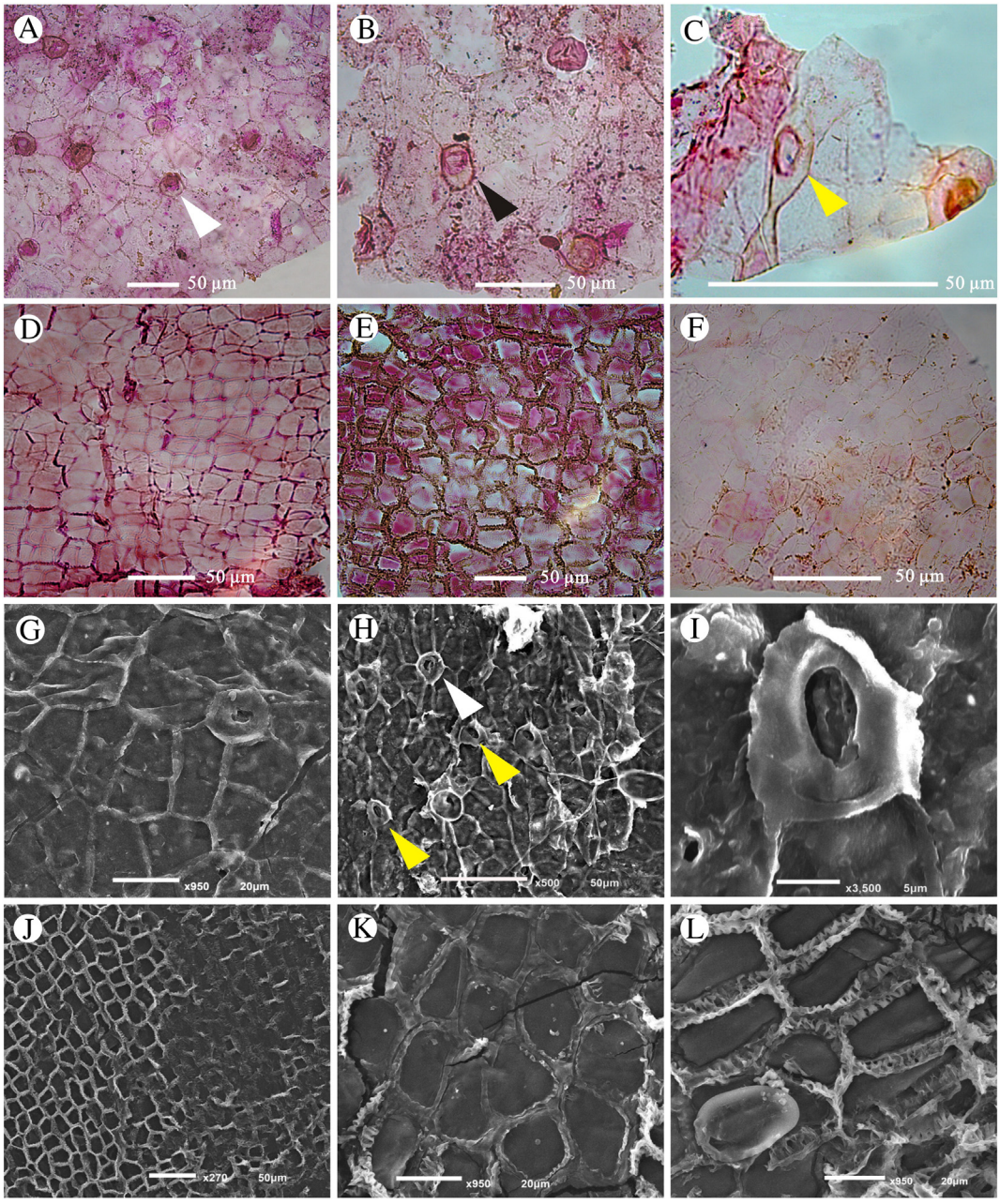

Fig. 5. *Burretiodendron guangxiensis* sp. nov. Illustrations of the wing and endocarp cuticles. (A–C) Cuticles of the wing by light microscopy showing a solitary rounded trichome base (white arrowhead), gland (black arrowhead) and anomocytic stoma (yellow arrowhead). (D–F) Cuticles of the endocarp by light microscopy showing fenstral fabric, quadrangle to pentagon cells. (G–I) Cuticles of the wing by SEM. (H) Showing anomocytic stomatal complex (yellow arrowheads). (I) Enlargement of oblong stoma from (H). (J–L) Cuticles of the endocarp by SEM.

coriaceous, and the endocarp of *Podopterus* is situated in the upper two-thirds of the fruit body (Anberrée et al., 2015). *Begonia* fruits vary from *Burretiodendron* by their larger locule region and elongated areoles of wing venation (O'Leary, 2007; Appendix 1).

The extant *Burretiodendron* fruits are distinctive schizocarp with five wings. The main veins fan outward into the wings from the elliptical central body and vein density is sparse. Generally, all the fossil specimens are similar to extant species in morphological characteristics but differ in overall size of the mericarp and endocarp (Table 1). Despite the unknown species *Burretiodendron brilletii*, the mericarp and endocarp size of the other five species are significantly larger and are approaching two times greater than that of *B. guangxiensis* sp. nov. However, *B. hsienmu* has a typical obovate fruit shape and a cuneate base that are consistent with the present fossils. The L/W ratio range of fruit body of the present fossils and *B. hsienmu* is close to the same. Hence, the extant species *B. hsienmu* is diagnosed as the nearest living relative of *B. guangxiensis* sp. nov., which is consistent with cluster analysis dendrogram performed by SPSS.

The fruit fossil record of *Burretiodendron* is scarce, and only one species, *B. parvifructum* J. Lebreton Anberrée & Z.K. Zhou, is reported from the upper Miocene Xiaolongtan Formation (Wenshan and Maguan) of southeastern Yunnan, China (Anberrée et al., 2015). *B. parvifructum* is elliptic to obovate, and the sizes of the mericarp and endocarp are similar to that of *B. guangxiensis* sp. nov. However, in *B. parvifructum*, the mericarp base is rounded and the distance between the base of the mericarp and the base of the endocarp is 3.8–4.4 mm. Hence, we diagnose these fruit fossils as a new species *B. guangxiensis* J.L. Dong et B.N. Sun sp. nov.

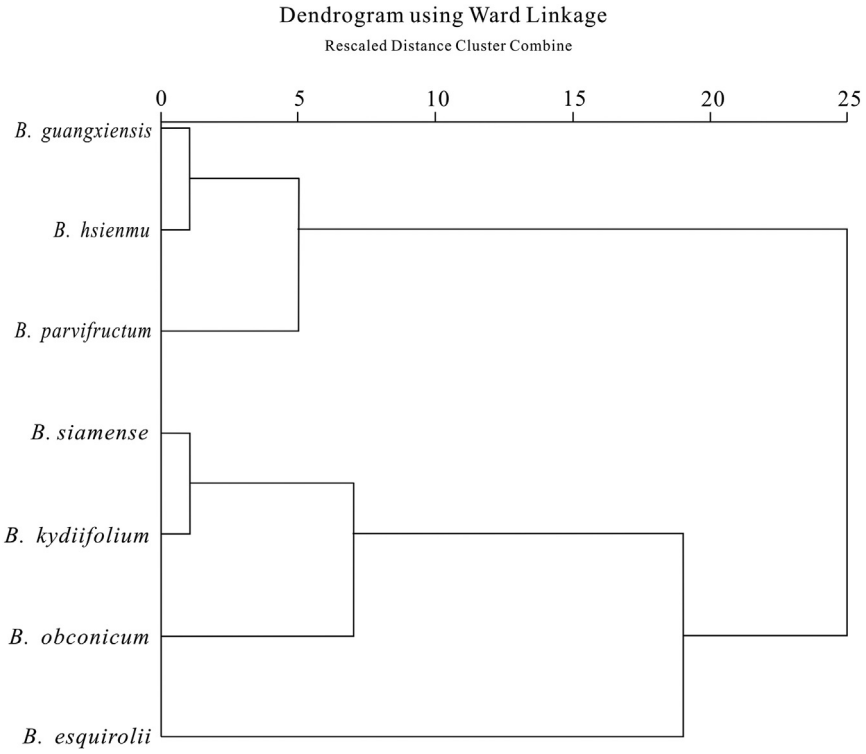

Fig. 6. The cluster analysis dendrogram performed by SPSS showing the relationship of the genus *Burretiodendron* between extant and fossil species.

4.2. Paleoclimatic indicator of Burretiodendron

We used the climate requirements of *Burretiodendron* to explore paleoclimate implication of the Ningming Formation in the Oligocene (Table 2). The mean annual temperature (MAT) is 15.0 °C to 27.5 °C and the mean annual precipitation values (MAP) range from 886 mm to 2067 mm. The precipitation of the warm quarter is 255–1146 mm, whereas winter is a period of relative drought with the precipitation of the cold quarter ranging from 42 mm to 279 mm (Anberrée et al., 2015). The result shows that the Ningming Formation formed under a warm and humid climate with seasonal precipitation. The current mean annual temperature (MAT) of the fossil site is 17.8 °C and the mean annual precipitation (MAP) is 1309.7 mm. The growing season precipitation (GSP) is 1167.1 mm and the mean precipitation of the coldest quarter is 118.2 mm. Hence, the climate conditions of the Ningming Formation during the Oligocene were likely warmer and more humid than the current conditions.)

Using the Coexistence Approach, Ma (2015) quantitatively reconstructed the paleoclimate of the Oligocene Ningming flora based on the macrofossils. The results indicate that the mean annual temperature was 18.9–22.4 °C and the mean annual precipitation was 1225.7–1592.0 mm, and the relative humidity was 78–82%. CLAMP data (Shi, 2010) showed that the reconstructed growing season precipitation was 1657 ± 200 mm and precipitation during the 3 consecutive wettest months was 814 ± 145 mm, and precipitation during the 3 consecutive driest months was 196 ± 32 mm. These data suggest that the Ningming Formation had a warm and humid climate and the precipitation was seasonal during the Oligocene. The Ningming paleoflora was mainly composed of Arecaceae, Fabaceae, Oleaceae, Juglandaceae, and Lauraceae (Shi et al., 2014; Wang et al., 2014; Ma, 2015; Dong et al., 2016; Ma et al., 2017; Wang et al., 2015, 2016) and represented tropical to subtropical vegetation, which exhibited a high species diversity in the Ningming paleoflora.

Quan et al. (2013) used modern global climatic data to examine the five indices based on temperature and precipitation with the benchmark of PET (potential evapotranspiration)-based HI (Thornthwaite humidity index), and finally validated the Köppen aridity index ($AI_{Köppen}$) for being the most reliable aridity index. $AI_{Köppen}$ is supported by the highest correlation coefficient respective to the Thornthwaite humidity index (HI), soil moisture index (SMI) and near-ground atmospheric relative humidity (RH). The formula of $AI_{Köppen}$ is the mean annual precipitation divided by the mean annual temperature plus a constant of 33 (Köppen, 1923). Hence, the Oligocene climate of the Ningming region can be considered humid with a mean $AI_{Köppen}$ of 26.24 (See Table 3).

$$AI_{Köppen} = \frac{MAP}{MAT + 33} \quad (1)$$

4.3. Ecological implication of Burretiodendron fruits

Anemochory is a relatively important mechanism of plant evolution and diversification in tropical rainforests (Herrera et al., 2014). Wind-dispersed fruits were already abundant in the Oligocene Ningming flora (Dong et al., 2016) and showed morphological diversity in terms of the structural adaptations for wind dispersal (e.g., dissemi-nules with one, two or three well-developed wings and fin-winged fruits). *Burretiodendron* has a septicidal capsule of five two-winged valves with an ecological adaptation for wind dispersal. Most living species of *Burretiodendron* have highly plant diversity in the upper canopy layer. Trees are >30 metres high and grow on high and steep topography. The growth environments are conducive to the wind dispersal of the genus *Burretiodendron*. However, after ripening of the fruit, the natural update is confined to under or around the canopy layer, and the fruit dispersal by wind is no >10 m (Gao, 2006). Furthermore, such small, nutrition-rich fruits and seeds still attract animal dispersants (mice and bats) in modern *Burretiodendron* fruits (Gao, 2006). Birds and bats are very abundant components and are also responsible for an important percentage of dispersed seeds in tropical–subtropical rainforests (Levey, 1988; Terborgh et al., 1990; Medellín and Gaona, 1999). As a result, animal dispersants may play a key role in long-distance seed

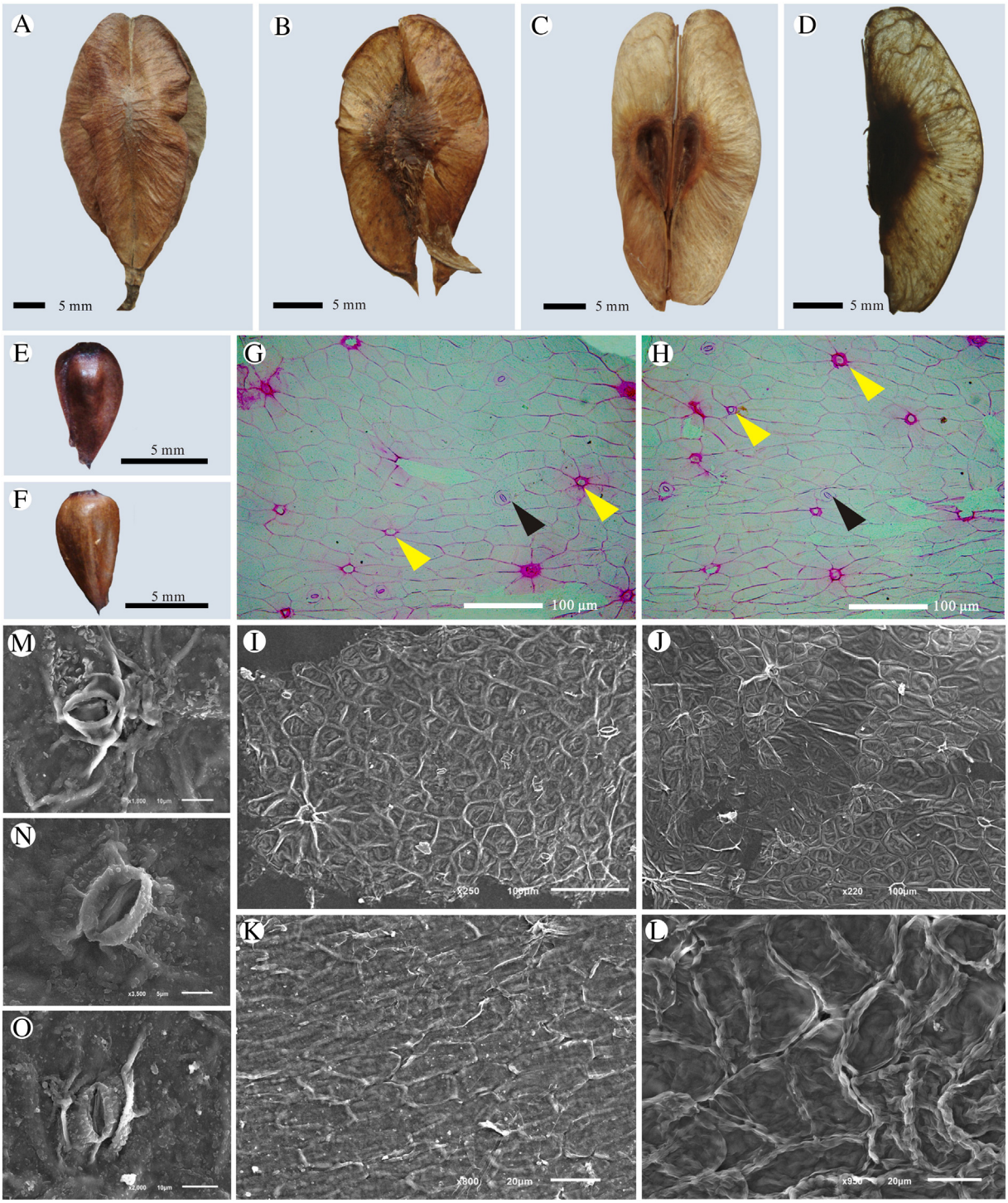

Fig. 7. *Burretiodendron hsienmu*. Extant. Fruit morphology and cuticles of the wing and endocarp. (A–F) Fruit morphology. (A) Intact fruit body. (B) Abaxial view. (C) Adaxial view. (D) Wing showing straight and stout primary vein running and wing venation radiating out from the endocarp area, craspedodromous, anastomosing and dichotomising but not forming elongated areoles. (E–F) Seed. (G–H) Cuticles of the wing by light microscopy showing rounded trichome bases (yellow arrowheads) surrounded by five to eight radial and wedge-shaped epidermal cells and oriented and anomocytic stoma (black arrowheads). (I–J) Cuticles of the wing by SEM. (K–L) Cuticles of the endocarp by SEM showing trichome bases (yellow arrowheads). (M–O) Enlargement of the anomocytic stoma by SEM.

dispersal of *Burretiodendron*, especially birds, mice and bats fed on seeds (Gopukumar et al., 2005; Ma et al., 2004; Tang et al., 2005c).

4.4. The significance of *Burretiodendron* as an indicator for karstification

From the Devonian to the Triassic, the sedimentary formation of Guangxi was mainly composed of thick and pure carbonate (Liu et al., 2001). From the end of the Middle Triassic to the Middle–Upper Triassic, the Indosinian Movement caused Guangxi to move away from the ocean into the terrestrial environment (Liu, 1993), which can provide necessary materials for the formation of the karst landform. From the late Triassic to the early Cenozoic, the tectonic movements continued to occur. The powerful fold deformations gave rise to rock fractures and cracks and joints, and this not only improved the secondary

Table 1
Morphological comparisons of the fossil and extant *Burretiodendron* fruits.

	Fruit outline					Endocarp				Fruit/Endocarp		D[a] (mm)	Wing venation	
	Shape	Base	L/mm[b]	W/mm[b]	L:W[b]	Shape	L/mm[b]	W/mm[b]	L:W[b]	FL/EL	FW/EW		Framework	Elongated areoles
Fossil species														
B. guangxiensis	Obovate	Cuneate	11.8–18.2	6.6–10.7	1.5–2.0	Obovate	4.4–6.5	3.0–4.6	1.2–1.7	2.3–3.1	2.0–2.8	4.0–6.5	Craspedodromous	Absent
B. parvifructum	Elliptic to obovate	Rounded	14.3–18.8	8.4–10.6	1.4–1.9	Obovate	5.7–8.5	3.6–6.2	1.0–1.9	2.1–2.4	1.6–1.9	3.8–4.4	Craspedodromous	Absent
Extant														
B. hsienmu	Obovate	Cuneate	34.1–35.8	20.7–21.4	1.6–1.7	Obovate	11.8–14.9	6.0–6.9	2.0–2.2	2.2–3.0	3.0–3.6	Na[c]	Craspedodromous	Absent
B. obconicum	Obovate to elliptic	Cuneate	42.5–45.1	18.8–21.5	2.0–2.4	Obovate	16.7–17.7	6.7–7.6	2.2–2.6	2.4–2.7	2.4–3.2	Na[c]	Craspedodromous	Absent
B. esquirolii	Elliptic to obovate	Rounded	29.0–49.9	11.0–23.4	2.5–3.1	Obovate to elliptic	12.0–13.5	4.0–5.2	2.5–3.0	2.1–4.2	2.1–5.9	Na[c]	Craspedodromous	Absent
B. siamense	Obovate to elliptic	Rounded	33.4–38.9	12.9–15.2	2.4–2.5	Obovate	7.9–8.3	4.5–5.0	1.6–1.7	4.0-–4.9	2.5–3.4	Na[c]	Craspedodromous	Absent
B. kydiifolium	Obovate to elliptic	Rounded	30.5–38.0	16.9–19.3	1.8–2.0	Obovate	9.8–11.3	5.6–6.7	1.7–1.8	2.6–3.9	2.5–3.4	Na[c]	Craspedodromous	Absent

[a] Means that the distance between the base of the mericarp and the base of the endocarp.
[b] Means that data of *B. parvifructum* and five extant species are from Anberrée et al. (2015).
[c] Means that data do not acquire.

permeability of the rocks, but also provided prerequisites for atmospheric precipitation infiltration and groundwater movements (Liu et al., 2001). The Ningming Basin is a Graben Basin along the NEE-trending great fracture distribution (Su et al., 1996). Currently, we still see the fault contact relationships between the Tertiary and the Permian and the Triassic strata in the Mingjiang North Shore that is 1.5 km from the Tuolong Village of Ningming County. The south of the fault is dominated by the Tertiary mudstone, whereas the north is dominated by the Permian and the Triassic limestone mountains (Kuang et al., 2004). Moreover, the Nonggang Karst Forest Nature Reserve is also located in the Tuolong Village of Ningming County.

Burretiodendron is a calcicolous tree species and survives by obtaining the necessary nutrients from rocks in the process of plant growth and development. Meanwhile, optimized growth for *Burretiodendron* is in high calcium containing alkali fertile moist soils (Wang, 2012), namely, a thick karst layer is most suited to support the growth of *Burretiodendron*. *Burretiodendron hsienmu*, the nearest living relative of *B. guangxiensis* sp. nov., is a characteristic species in karst seasonal rainforests (Zhuge, 1990) and exclusively grows in the limestone regions south of the Tropic of Cancer (Wang et al., 1998; Tang et al., 2005b; Li et al., 2008). *B. hsienmu* belongs to the climax communities in the floristics (Zheng, 1999), whereas the appearance of climax vegetation in karst areas indicates the formation of climax topography and soils (Li, 2002). Jennings (1985) deemed that vegetation and soils of the limestone surface are one of most important factors affecting the surface erosion of limestone. Thus, the discovery of *B. guangxiensis* sp. nov. implies the presence of a karstic system, already in the Oligocene Ningming Formation.

Furthermore, the Ningming paleoflora existed under a warm and humid tropical–subtropical climate with seasonal precipitation and the activity of the surface water was intense. These climate conditions favour the formation of the karst landform. Moreover, the CO_2 was 255 to 972 ppmv during the development of the Ningming Formation (Sun et al., 2016), which was conducive to the dissolution of carbonate rocks. Thus, the identified *Burretiodendron guangxiensis* sp. nov. from the Oligocene Ningming Formation, Guangxi, may indicate that karst landforms might have been intensively developed in the Oligocene.

5. Conclusions

1) The fossil records of *Burretiodendron* Rehder are reviewed based on diagnostic winged fruits from the Oligocene Ningming Formation, Guangxi, South China.
2) The paleoclimate of Ningming Region was a warm and humid climate with seasonal precipitation during the Oligocene.
3) The ecological adaptation of *Burretiodendron* occurred through wind dispersal, but animal dispersants may play a key role in long-distance seed dispersal of *Burretiodendron*.
4) Edaphic preferences of the NLR identified for the fossil species may point to the existence of a karstic system in the Ningming Region during the Oligocene.

Acknowledgments

We thank Dr. De-Fei Yan, Dr. San-Ping Xie, and Dr. Jing-Yu Wu for the constructive comments. We are also grateful to Dr. Dian-Xiang Zhang and Dr. Fei-Yan Zeng for their permission to access the extant *Burretiodendron* specimens for comparison. This work was supported by the National Natural Science Foundation of China (grant number 41172022) and the Fundamental Research Funds for the Central Universities (No. lzujbky-2014-285) and the US Louisiana Board of Regents under grant LEQSF (2017-20)-RD-A-29 to MXS.

Table 2
Climatic parameters of extant *Burretiodendron*.

	MAT (°C)	MAP (mm)	PWETM (mm)	PDRYM (mm)	PCQ (mm)	PWQ (mm)
Range	15.0–27.5	886–2067	158–424	4–48	42–279	255–1146
Mean ± SD	21.7 ± 2.9	1476 ± 256	280 ± 54	18 ± 10	95 ± 56	701 ± 203

Data are from Anberrée et al. (2015). MAT, mean annual temperature; MAP, mean annual precipitation; PWETM, precipitation of wettest month; PDRYM, precipitation of driest month; PCQ, precipitation of coldest quarter; PWQ, precipitation of warmest quarter.

Table 3
Categories of the climate condition based on the $AI_{Köppen}$.

Hyper-arid	Arid	Semi-arid	Sub-humid	Humid
<0.9	0.9–5.7	5.7–13.6	13.6–15.6	>15.6

Data are from Quan et al. (2013).

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.palaeo.2017.07.004.

References

Alverson, W.S., Whitlock, B.A., Nyffeler, R., Bayer, C., Baum, D.A., 1999. Phylogeny of the core Malvales. Am. J. Bot. 86, 1474–1486.

Anberrée, J.L., Manchester, S.R., Huang, J., Li, S.F., Wang, Y.Q., Zhou, Z.K., 2015. First fossil fruits and leaves of *Burretiodendron* s.l. (Malvaceae s.l.) in southeast Asia: implications for taxonomy, biogeography, and paleoclimate. Int. J. Plant Sci. 176 (7), 682–696.

Bayer, C., Fay, M.F., Bruijn, A.Y.D.E., Savolainen, V., Morton, C.M., Kubitzki, K., Alverson, W.S., Chase, M.W., 1999. Support for an expanded family concept of "Malvaceae" within a recircumscribed order Malvales: a combined analysis of plastid atpB and rbcL DNA sequences. Bot. J. Linn. Soc. 129, 267–303.

Bell, C.D., Soltis, D.E., Soltis, P.S., 2010. The age and diversification of the angiosperms re-revisited. Am. J. Bot. 97, 1296–1303.

Bůžek, C., Kvaček, Z., Manchester, S.R., 1989. Sapindaceous affinities of the *Pteleaecarpum* fruits from the Tertiary of Eurasia and North America. Bot. Gaz. 150, 477–489.

Cao, J.H., Yuan, D.X., Pan, G.X., Lin, Y.S., 2001. Preliminary study on biological action in karst dynamic system. Earth Sci. Front. 8 (1), 203–209 (in Chinese with English abstract).

Chang, H.T., Miau, R.H., 1978. The taxonomy of Excentrodendroideae, Tiliaceae. Acta Sci. Nat. Univ. Sunyatseni 53, 19–26 (in Chinese).

Chen, G.J., Chang, M.M., 2011. A new cyprinin from Oligocene of South China. Sci. China Earth Sci. 54, 481–492.

Chen, G.J., Fang, F., Chang, M.M., 2005. A new cyprinid closely related to cultrins + xenocyprinins from the Mid-Tertiary of South China. J. Vertebr. Paleontol. 25, 492–501.

Chun, W., How, K.C., 1956. Species novae arborum utilium Chinae meridionalis. Acta Phytotaxon. Sin. 5, 1–18 (in Chinese).

Conover, M.V., 1991. Epidermal patterns of the reticulate-veined Liliiflorae and their parallel-veined allies. Bot. J. Linn. Soc. 107, 295–312.

Deng, Z.Q., 1982. On the effect of plant activities upon the tropical karst development case history of the Longang Nature Conservation region. Carsologica Sin. 1, 49–58 (in Chinese with English abstract).

Dong, J.L., Sun, B.N., Ma, F.J., Wang, Q.J., Jin, P.H., Wang, W.J., Yang, Y., Li, X.J., 2015. *Paliurus* fruits from the Oligocene of South China and their phytogeographic implications. PLoS One 10 (11), e0140653.

Dong, J.L., Wang, W.J., Deng, P., Wang, J., Ma, F.J., Wang, Q.J., Yang, Y., Sun, B.N., 2016. New material of *Palaeocarya* from the Oligocene of Ningming, Guangxi, South China. Paläontol. Z. 90, 399–412.

Eisenhauer, N., Scheu, S., Jousset, A., 2012. Bacterial diversity stabilizes community productivity. PLoS One 7 (3), e34517.

Gao, H., 2006. A Biological Study of *Excentrodendron hsienmu* H.T. Chang and R.H. Miau and its Significance in Conservation Ecology. (Ph.D. Dissertation). Sichuan University Sichuan, in Chinese with English abstract.

Gopukumar, N., Karuppudurai, T., Swami Doss, D.P., 2005. Dispersal patterns of the short-nosed fruit bat *Cynopterus sphinx* (Chiroptera: Pteropodidae). Mamm. Biol. 70 (2), 22–125.

Hamilton, E.W., Frank, D.A., 2001. Can plants stimulate soil microbes and Diuglas A. Frank. Ecology 82 (9), 2397–2402.

Harris, J.G., Harris, M.W., 2001. Plant Identification Terminology: Payson Utah.

Herrera, F., Manchester, S.R., Carvalho, M.R., Jaramillo, C., Wing, S.L., 2014. Paleocene wind-dispersed fruits and seeds from Colombia and their implications for early Neotropical rainforests. Acta Palaeobot. 54 (2), 197–229.

Jennings, J.N., 1985. Karst Geomorphology. Basil Blace-well Ltd, Oxford, U.K.

Judd, W.S.W., Manchester, S.R., 1997. Circumscription of Malvaceae (Malvales) as determined by a preliminary cladistic analysis of morphological, anatomical, palynological, and chemical characters. Brittonia 49, 384–405.

Köppen, W., 1923. Die Klimate der Erde. Walter de Gruyter&Co, Berlin und Leipzig.

Kostermans, A.J.G., 1961. The genus *Burretiodendron* Rehder. Reinwardtia 6, 1–16.

Kuang, G.D., Chen, G.J., Chen, Y.F., Huang, Z.T., 2004. New information on the tertiary biostratigraphy of the Ningming Basin, Guangxi. J. Stratigr. 28, 362–367 (in Chinese with English abstract).

Kvaček, Z., Bůžek, C., Manchester, S.R., 1991. Fossil fruits of *Pteleaecarpum* Weyland-Tiliaceous, not Sapindaceous. Bot. Gaz. 152, 522–523.

Levey, D.J., 1988. Tropical wet forest treefall gaps and distribution of understory birds and plants. Ecology 69, 113–122.

Li, E.X., 2002. The Characteristics of Eco-factors Under Different Karst Vegetations in the Process of Succession. (Master Dissertation). Guangxi Normal University, Guangxi in Chinese with English abstract.

Li, X.K., Su, Z.M., Lu, S.H., O, Z.L., Xing, W.S., Qu, Z., Chen, S.H., 2003. The spatial pattern of natural vegetation in the karst regions of Guangxi and the ecological signality for ecosystem rehabilitation and reconstruction. J. Mt. Sci. 21 (2), 129–136 (in Chinese with English abstract).

Li, J.H., Tang, Y., Shoup, S., 2004. Sequences of nrDNA support *Excentrodendron* and *Burretiodendron* (Malvaceae). Harv. Pap. Bot. 9 (1), 83–88.

Li, X.K., Jiang, Z.C., Huang, Y.Q., Xiang, W.S., Lv, S.H., Ye, D., Su, Z.M., 2008. Dynamics of dominant population and its influence on Karstification in Southwest Guangxi, China. Acta Geosci. Sin. 29 (2), 253–259 (in Chinese with English abstract).

Liu, B.J., 1993. Evolution and Mineralization of Continental Crust in Southern China. Science Press, Beijing (in Chinese).

Liu, J.R., Huang, G.B., Huang, X.L., Liang, Y.C., 2001. Discussion on the evolution of different types of regional tropical karst landform in Guangxi. Carsologica Sin. 20 (4), 247–252 (in Chinese with English abstract).

Long, H., He, L.K., Hsue, H.H., 1985. Pollen morphology of *Craigia* with reference to its systematic position. Acta Phytotaxon. Sin. 23, 179–184 (in Chinese with English abstract).

Ma, F.J., 2015. Angiosperm Fossils From the Oligocene of Ningming, Guangxi and a Paleoclimatic Reconstruction of the Flora. (Ph.D. Dissertation). Lanzhou University, Lanzhou in Chinese with English abstract.

Ma, J., Zhang, J.G., Zhang, E.Q., Zhang, J.S., Liang, B., Zhang, S.Y., Shen, J.X., 2004. Important role of flying foxes (Megachiroptera) to forest ecosystem. Chin. J. Ecol. 23 (3), 115–119 (in Chinese with English abstract).

Ma, F.J., Wang, Q.J., Dong, J.L., Yang, Y., Wang, W.J., Yan, D.F., Sun, B.N., 2015. *Buxus* leaves from the Oligocene of Guangxi, China and their biogeographical significance. Acta Geol. Sin. (Engl. Ed.). 89 (5), 1453–1469.

Ma, F.J., Sun, B.N., Wang, Q.J., Dong, J.L., Yang, Y., Yan, D.F., 2016. A new species of *Zelkova* (Ulmaceae, Ulmoideae) with leaves and fruits from the Oligocene of South China and its biogeographical implications. Hist. Biol. 29 (1), 1–10.

Ma, F.J., Liu, S., Sun, B.N., Yan, D.F., Dong, J.L., Zhang, F.T., Wang, Q.J., 2017. Legume fruits from the Oligocene Ningming Formation of Guangxi, China, and their biogeographical and palaeoclimatic implications. Rev. Palaeobot. Palynol. 244, 192–202.

Manchester, S.R., O'Leary, E.L., 2010. Phylogenetic distribution and identification of fin-winged fruits. Bot. Rev. 76, 1–82.

Medellín, R.A., Gaona, O., 1999. Seed dispersal by bats and birds in forest and disturbed habitats of Chiapas, México. Biotropica 31 (3), 478–485.

Ning, Z.S., Zhou, T.M., Hu, Y.K., Liang, Z.H., 1994. Tertiary in Petroliferous Regions of China. Petroleum Industry Press, Beijing (in Chinese).

O'Leary, E.L., 2007. Taxonomic Distribution of Modern Fin-winged Fruits and the Fossil History of the Combretaceae in the United States Based on Fin-winged Fruits. (Master of Science Thesis). University of Florida, Gainesville.

Quan, C., Han, S., Utescher, T., Zhang, C.H., Liu, Y.S., 2013. Validation of temperature–precipitation based aridity index: Paleoclimatic implications. Palaeogeogr. Palaeoclimatol. Palaeoecol. 386, 86–95.

Rehder, A., 1936. *Burretiodendron*, a new genus of Tiliaceae. J. Arnold Arbor. Harv. Univ. 17, 49.

Shi, G.L., 2010. Fossil Plants From the Oligocene Ningming Formation of Guangxi, and a Preliminary Palaeoclimatic Reconstruction of the Flora. (Master'Dissertation). Nanjing Institute of Palaeontology and Geology, Chinese Academy of Sciences, Nanjing in Chinese with English abstract.

Shi, G.L., Zhou, Z.Y., Xie, Z.M., 2010. A new *Cephalotaxus* and associated epiphyllous fungi from the Oligocene of Guangxi, South China. Rev. Palaeobot. Palynol. 161, 179–195.

Shi, G.L., Xie, Z.M., Li, H.M., 2014. High diversity of Lauraceae from the Oligocene of Ningming, South China. Palaeoworld 23, 336–356.

Su, Z.Y., Liao, W.B., Chang, H.T., 1996. Vegetational and floristic characteristics of Guangxi I. Natural Conditions and Floristic Composition. Suppl. J. Sun Yat-sen Univ. 2, 81–86 (in Chinese with English abstract).

Sun, B.N., Wang, Q.J., Konrad, W., Ma, F.J., Dong, J.L., Wang, Z.X., 2016. Reconstruction of atmospheric CO_2 during the Oligocene based on leaf fossils from the Ningming Formation in Guangxi, China. Palaeogeogr. Palaeoclimatol. Palaeoecol. 467, 5–15.

Tang, Y., Gao, X.F., 1993. Pollen morphology of *Burretiodendron* sensu lato (Tiliaceae) and its systematic significance. Cathaya 5, 81–88.

Tang, Y., Xie, J.S., Gao, H., 2005a. A study of wood anatomy of *Burretiodendron* Rehder and *Excentrodendron* H. T. Chang & R. H. Miau and its systematic implications. Acta Bot. Yunnanica 27, 235–246 (in Chinese with English abstract).

Tang, Y., Mao, L.H., Gao, H., 2005b. Over-exploitation and lack of protection is leading to a decline of a protected calcicolous tree species (Tiliaceae) in China. Biol. Conserv. 126, 14–23.

Tang, Z.H., Cao, M., Sheng, L.X., Liang, B., Zhang, S.Y., 2005c. Fruit consumption and seed dispersal of wild banana *Musa acuminata* by short-nosed fruit bat *Cynopterus sphinx*. Acta Zool. Sin. 51 (4), 608–615 (in Chinese with English abstract).

Terborgh, J., Robinson, S.K., Parker III, T.A., Munn, C.A., Pierpont, N., 1990. Structure and organization of an Amazonian forest bird community. Ecol. Monogr. 60, 213–238.

Wang, B., 2012. Ecological Study of *Excentrodendron hsienmu* Community in North Tropical Karst Seasonal Rainforest. (Master Dissertation). Guangxi Normal University, Guangxi in Chinese with English abstract.

Wang, X., Jin, X., Sun, C., 1986. *Burretiodendron hsienmu* Chun & How: its ecology and its protection. Arnoldia 46, 46–51.

Wang, X.P., Sun, S.Z., Li, X.X., 1998. Study of limestone seasonal rain forest classification in Guangxi. Bull. Bot. Res. 18 (4), 428–447 (in Chinese with English abstract).

Wang, W.M., Chen, G.J., Chen, Y.F., Kuang, G.D., 2003. Tertiary palynostratigraphy of the Ningming Basin, Guangxi. J. Stratigr. 27, 324–327 (in Chinese with English abstract).

Wang, Q., Song, Z.Q., Chen, Y.F., Shen, S., Li, Z.Y., 2014. Leaves and fruits of *Bauhinia* (Leguminosae, Caesalpinioideae, Cercideae) from the Oligocene Ningming Formation of Guangxi, south China and their biogeographic implications. BMC Evol. Biol. 14 (1), 1–17.

Wang, Q.J., Ma, F.J., Dong, J.L., Yang, Y., Jin, P.H., Sun, B.N., 2015. Coryphoid palms from the Oligocene of China and their biogeographical implications. C.R. Palevol. 14, 263–279.

Wang, Q.J., Ma, F.J., Dong, J.L., Liu, C.H., Liu, S., Sun, B.N., 2016. New costapalmate palm leaves from the Oligocene Ningming formation of Guangxi, China, and their biogeographic and palaeoclimatic implications. Hist. Biol. 29, 594–606.
Won, H., 2009. Phylogenetic position of *Corchoropsis* Siebold & Zucc. (Malvaceae s.l.) inferred from plastid DNA sequences. J. Plant Biol. 52, 411–416.
Yin, H.F., Xie, S.C., Zhou, X.G., 1994. Advances and trends on the study of microbial metallogenesis. Earth Sci. Front. 1 (3/4), 148–156 (in Chinese with English abstract).
Yuan, D.X., 1997. Modern karst and global change research. Earth Sci. Front. 4 (1), 17–25 (in Chinese with English abstract).
Yuan, D.X., 2001. On the karst ecosystem. Acta Geol. Sin. 75 (3), 336–338.
Zhang, F.R., 1992. Soil Genesis and Taxonomy. Peking University Press (in Chinese).
Zheng, Y.W., 1999. Introduction to Mulun Karst Forest Region. Science Press, Beijing (in Chinese).
Zhuge, R., 1990. On the genus *Burretiodendron* sensu lato (Tiliaceae). J. Arnold Arbor. Harv. Univ. 71, 371–380.